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La Ferrassie 1: New perspectives on a "classic" Neandertal

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ABSTRACT

The La Ferrassie 1 (LF1) skeleton, discovered over a century ago, is one of the most important Neandertal individuals both for its completeness and due to the role it has played historically in the interpretation of Neandertal anatomy and lifeways. Here we present new skeletal remains from this individual, which include a complete right middle ear ossicular chain (malleus, incus, and stapes), three vertebral fragments, and two costal remains. Additionally, the study of the skeleton has allowed us to identify new pathological lesions, including a congenital variant in the atlas, a greenstick fracture of the left clavicle, and a lesion in a mid-thoracic rib of unknown etiology. In addition, we have quantified the amount of vertebral pathology, which is greater than previously appreciated. We have complemented the paleopathological analysis with a taphonomic analysis to identify any potential perimortem fractures. The taphonomic analysis indicates that no surface alteration is present in the LF1 skeleton and that the breakage pattern is that of bone that has lost collagen, which would be consistent with the intentional burial of this individual proposed by previous researchers. In this study, we used CT and microCT scans in order to discover new skeletal elements to better characterize the pathological lesions and to quantify the fracture orientation of those bones in which the current plaster reconstruction did not allow its direct visualization, which underlines the broad potential of imaging technologies in paleoanthropological research. A century after its discovery, LF1 is still providing new insights into Neandertal anatomy and behavior.

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1. Introduction

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New analytical and conceptual tools are providing the opportunity for paleoanthropologists to gain insights into fossil remains discovered a long time ago. Computed Tomography (CT) and microCT scans are providing new means to assess the fossil record, including the quantification of some anatomical features that were not previously (easily) accessible (e.g., Spoor et al., 1994; Stoessel et al., 2016a, b). These new technical means have also enlarged the available fossil record of certain bones that are not easily preserved, such as the ear ossicles (e.g., Gómez-Olivencia et al., 2015; Stoessel et al., 2016b), and have allowed researchers to develop novel approaches to studying the paleobiology of Pleistocene populations (Martínez et al., 2004, 2013; Quam et al., 2015).

At the same time, paleopathological and taphonomic approaches to hominin fossils represent complementary avenues of

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inquiry that, in combination, could be considered paleoforensic studies. These new approaches have already provided insights into important questions in human evolutionary studies. In particular, they are helping to clarify the anthropic origin of the Middle Pleistocene hominin accumulation at the site of the Sima de los Huesos (SH) in Spain (Arsuaga et al., 1990, 1997, 2014, 2015; Andrews and Fernández-Jalvo, 1997; Carbonell and Mosquera, 2006; Sala et al., 2014, 2015a, b, 2016). New excavations are providing evidence that complete human skeletons were accumulated in the SH (Arsuaga et al., 2014, 2015). Carnivores have been ruled out of the bone accumulation of the SH, as the carnivore activity on both bear and human bones at this site was subtle and performed by bears, which do not accumulate bones (Sala et al., 2014). Also, the SH human crania and long bones show a post-mortem fracture pattern, compatible with collective burial assemblages (Sala et al., 2015a, b; 2016). Also, new taphonomic analyses have also given rise to an interesting debate about the accumulation of Homo naledi hominins at Dinaledi Chamber in South Africa (Dirks et al., 2015; Val, 2016). They are also providing new insights into the potential cause-ofdeath of iconic fossil specimens such as A.L. 288-1 "Lucy" (Kappelman et al., 2016). In these two cases, breakage analysis provided an additional tool in order to complement classical paleopathological analyses as it provides information on whether a bone was broken around the time of the death (perimortem) or after death (postmortem) once the collagen was lost (Sala et al., 2015a, b; 2016). In this context, in order to assess the breakage patterns, new imaging techniques based on CT-scans were used. The ongoing reassessment of the faunal collections from "classical" Neandertal sites (e.g., Spy, Regourdou, Goyet, Combe Grenal) has led to the identification of new fossil remains. Coupled with new dating and imaging technologies, as well as new taphonomic approaches, this is providing novel and important data on Neandertals (e.g., Crevecoeur et al., 2010; Gómez-Olivencia et al., 2013a, b; Maureille et al., 2015; Rougier et al., 2016). The recent reassessment of the faunal remains associated with the La Ferrassie 1 (LF1) Neandertal skeleton at the Musée de l'Homme (MH, Museum national d'Histoire naturelle, Paris) led to the identification of five new skeletal elements belonging to this individual. LF1 was found in 1909 and was removed from the site in at least two blocks of sediment (which also included stone tools and faunal remains) sealed in plaster and subsequently cleaned at the Musée de l'Homme by Marcellin Boule (Laville, 2007). The new fossils from LF1 correspond to three vertebral fragments and two costal remains that have not been included in any previous studies.

This reassessment of the LF1 skeleton from an anatomical and taphonomic perspective also resulted in identifying previously undescribed bone anomalies in the axial and appendicular skeleton and provided the first taphonomic characterization of the LF1 skeleton. In addition, microCT scanning of the right temporal bone of LF1 led to the identification and virtual reconstruction of a complete ossicular chain (malleus, incus, and stapes) from the right side [Supplementary online material (SOM).stl files; SOM Fig. S1].

The present study provides the first metric and morphological description of these new LF1 fossils, as well as comparison with other Pleistocene and recent humans. In addition, the bone anomalies are described and discussed in the context of previous pathologies documented for this same individual. A complete taphonomic analysis of the LF1 individual is also provided, with an emphasis on timing and causes of bone breakage that would complete the paleopathological assessment and might have implications for LF1's status as an intentional burial. These new results have implications for Neandertal anatomical variation and evolution, the paleobiology of the LF1 individual, and the taphonomic

history of LF1 within the important archaeological sequence of the La Ferrassie rockshelter (Grand abri de la Ferrassie in French).

1.1. The La Ferrassie 1 skeleton

La Ferrassie rockshelter is located at the base of a limestone hill (Savignac de Miremont, Dordogne), five kilometers north of Le Bugue, France, This site preserves an important Middle and Upper Paleolithic sequence starting in MIS 5 (Turg et al., 2012; Guérin et al., 2015; Frouin et al., 2017). On 17 September 1909, an adult male Neandertal skeleton, designated La Ferrassie 1 (LF1), was recovered from what Denis Peyrony considered a funeral pit contemporary to level C (Maureille and Van Peer, 1998). The following year, a second skeleton was found 50 cm west of LF1 (for a complete description of the history of the findings and the context see Heim [1976], Laville [2007], and references therein). This second skeleton belonged to an adult woman and was designated La Ferrassie 2 (LF2). These two skeletons were used as comparative (and complementary) specimens by Boule in his famous monograph on the La Chapelle-aux-Saints 1 specimen (Boule, 1911–13). The specimens LF1 and LF2 were later thoroughly described in a two-volume monograph (Heim, 1976, 1982b).

From 1912 to 1921, the remains of another four immature individuals were recovered from La Ferrassie: La Ferrassie 3, 4bis, 5, and 6 (Heim, 1982a). The right humerus and femur that were once labeled as La Ferrassie 4 actually belong to the Le Moustier 2 skeleton (Maureille, 2002), and thus LF4bis could now be named LF4. Finally, in 1970 and 1973, a fifth immature individual was found, La Ferrassie 8 (Heim, 1982a). Recent reassessment of the materials from the excavations by Delporte have yielded new remains from La Ferrassie 8 (Gómez-Olivencia et al., 2015) and several isolated dental remains that appear to represent additional adult individuals (Becam et al., 2015).

All the LF skeletons were intentionally buried according to Peyrony (1934) and Heim (1976). In fact, a report written by D. Peyrony in 1920 to the Ministère des Beaux-Arts explains that all five skeletons discovered until that moment show more or less the same orientation (East-West). The two adults (LF1 and LF2) had their heads about 50 cm apart (Peyrony, 1934): LF2's head was located to the East and that of LF1 to the West. Moreover, the recent re-study of the archives from the different excavation periods show that LF1, LF2, and LF8, the three individuals for which more detailed information is available, had their head at a higher elevation than the rest of the body (Laville, 2007; Balzeau et al., 2016a, b). H. Breuil described LF1 as laying on an apparently natural depression (Maureille and Van Peer, 1998). D. Peyrony and M. Boule observed small packets of yellow sand (from the lower level) mixed with the Mousterian sediments associated with both LF1 and LF2, something not seen in the rest of the Mousterian levels. This has been interpreted as the effect of intentional funerary pits that removed sediment from the underlying level and mixed with that which afterwards filled the pit (Maureille and Van Peer, 1998). Both LF1 and LF2 are associated with the Ferrassie facies of the Mousterian. The geological levels they were discovered in are attributed to MIS3, between 54 ± 3 and 40 ± 2 ka (Guérin et al., 2015).

LF1 is a virtually complete skeleton that preserves all anatomical regions (Heim, 1976, 1982b; Fennell and Trinkaus, 1997; see SOM Table S1 and SOM Fig. S2). The bones missing in this skeleton are basically the patellae and small hand and foot bones. First, the presence of LF1 was recognized as a human femur and a human tibia were identified in the stratigraphic section. It is likely that one of the patellae was lost in the excavation that led to the unearthing of that stratigraphic section. The rest of the missing bones were either lost during the excavation process and/or were broken, which would have worsened their identifiability. It was determined

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